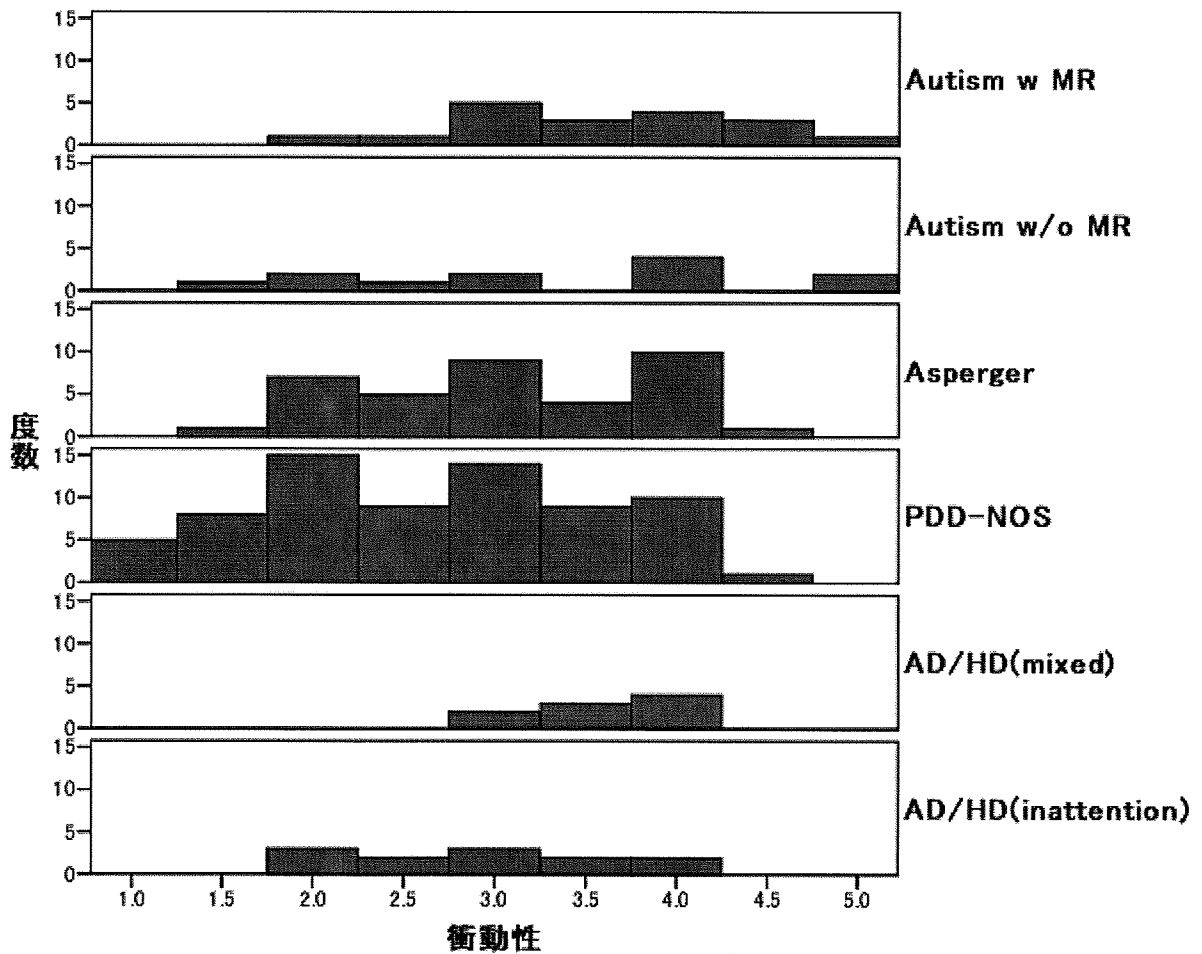
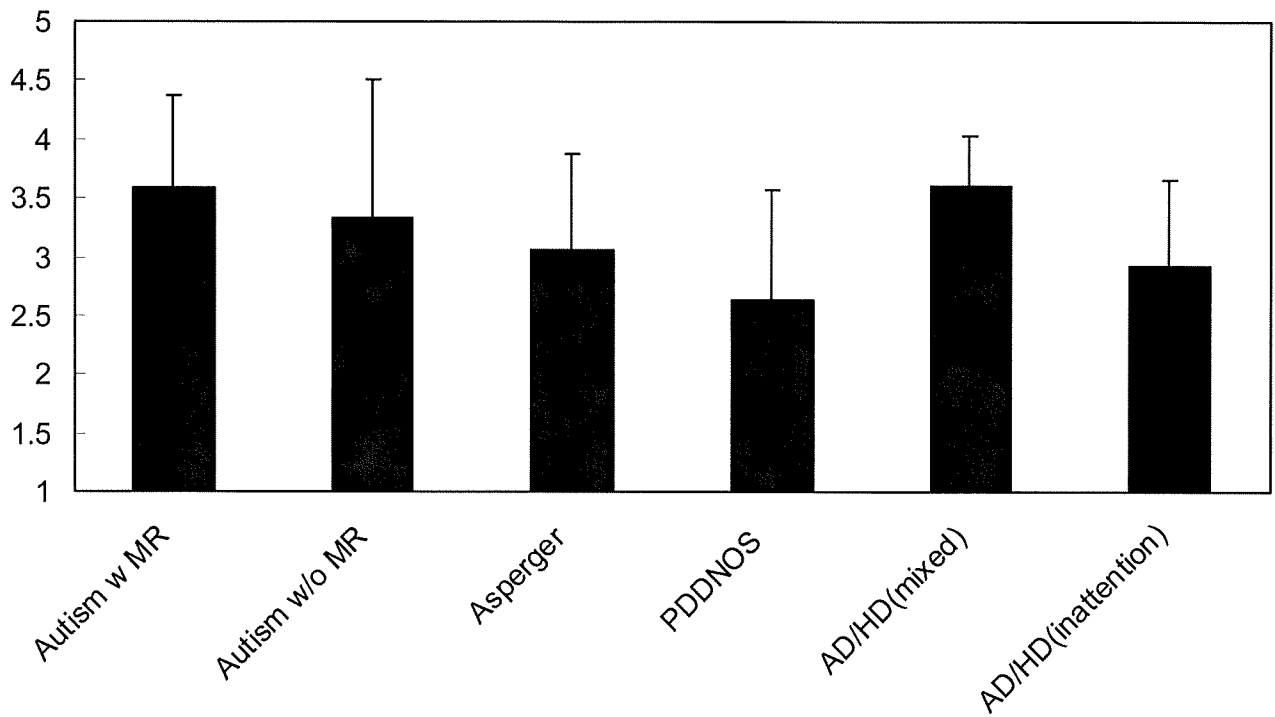


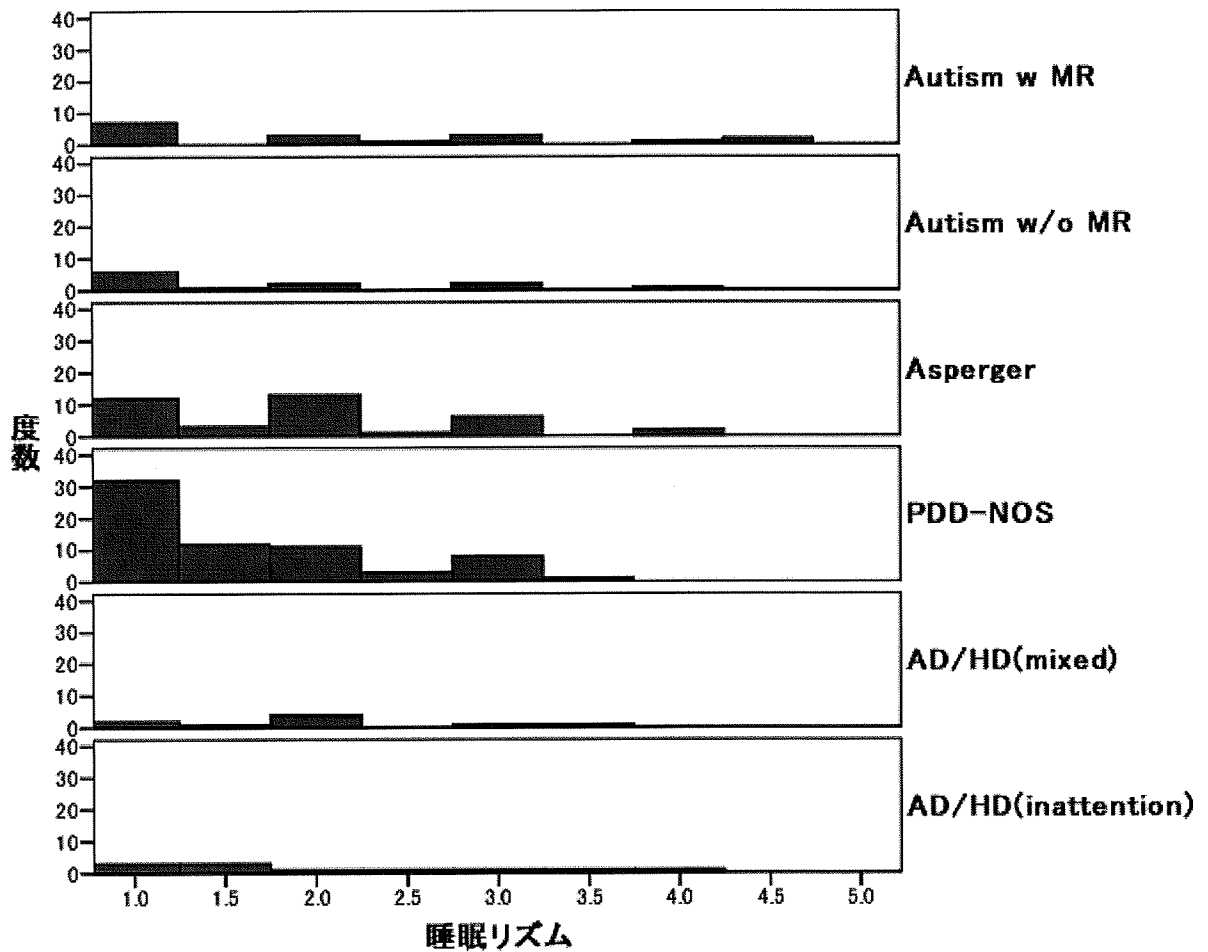
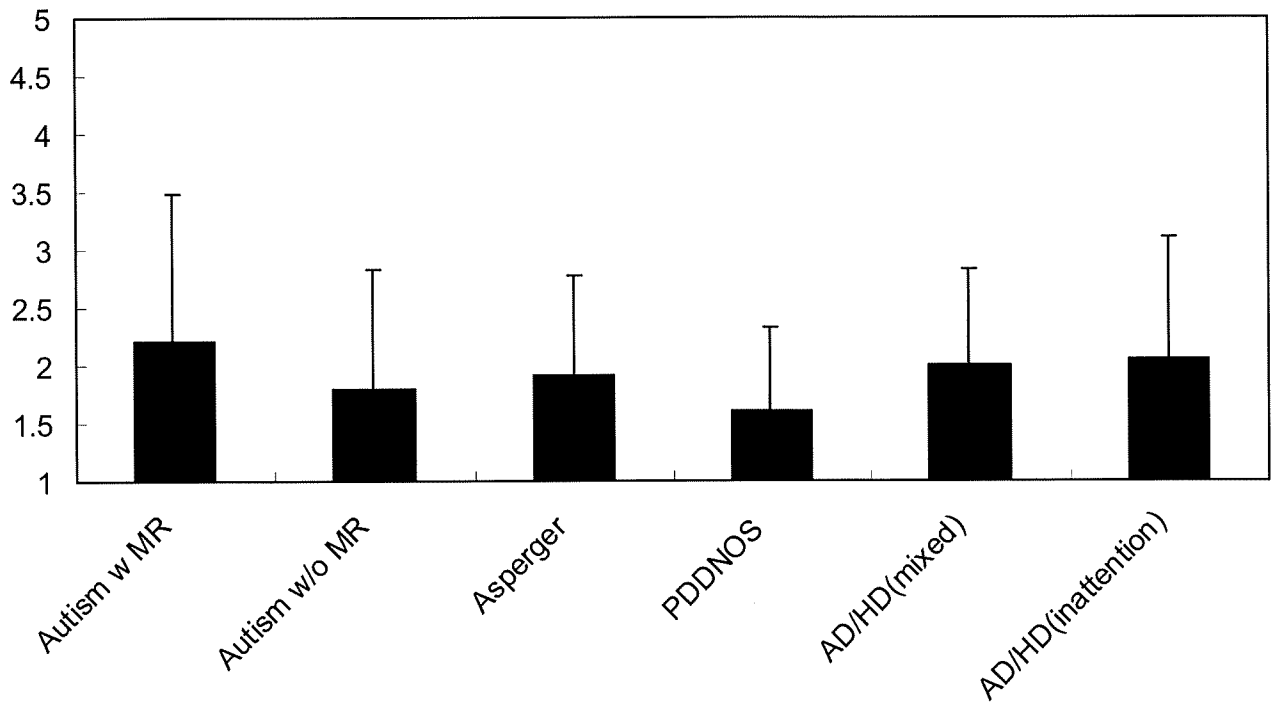
衝動性



PDD-NOS 群がやや低めであるが、いずれの群も衝動性という点において、困り度は高いようである。群間差としては、PDD-NOS 群が知

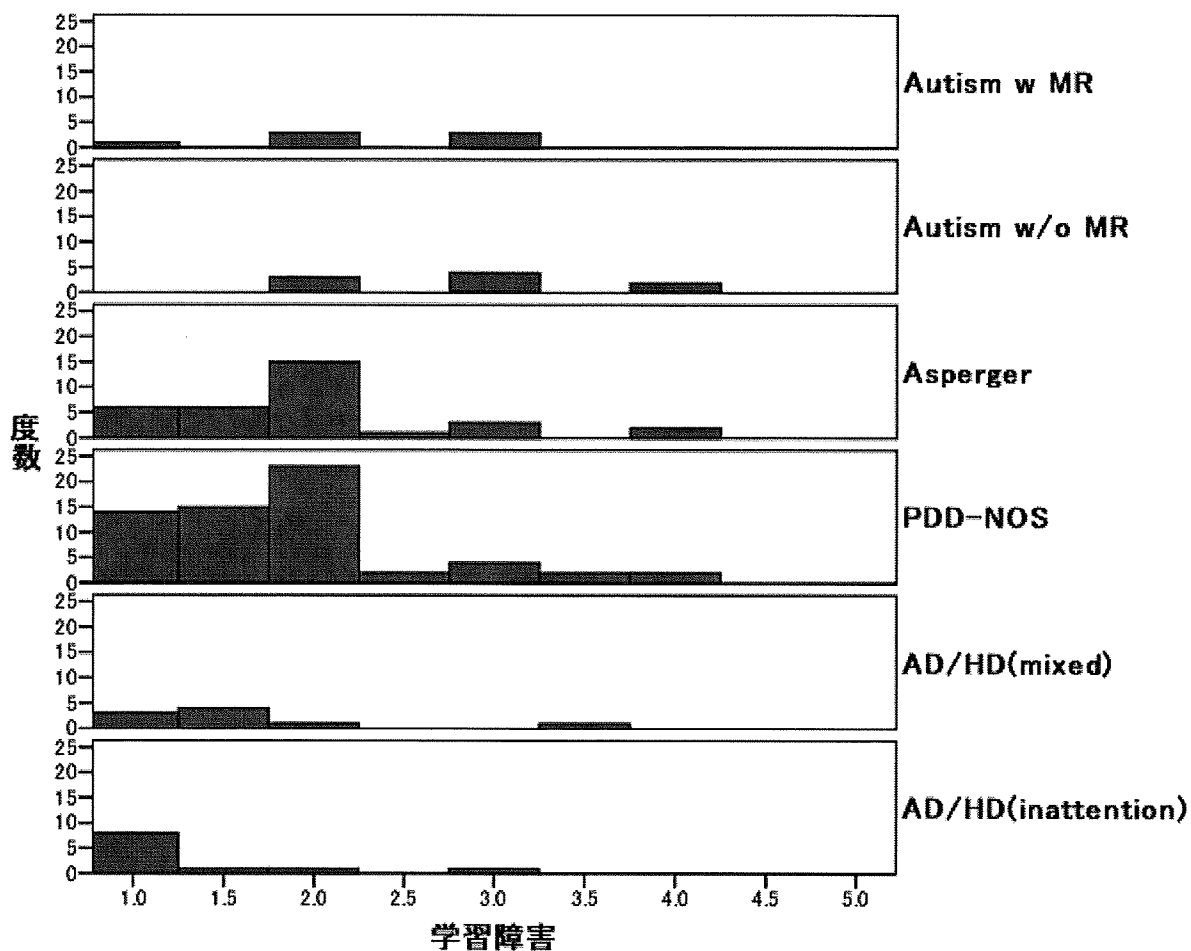
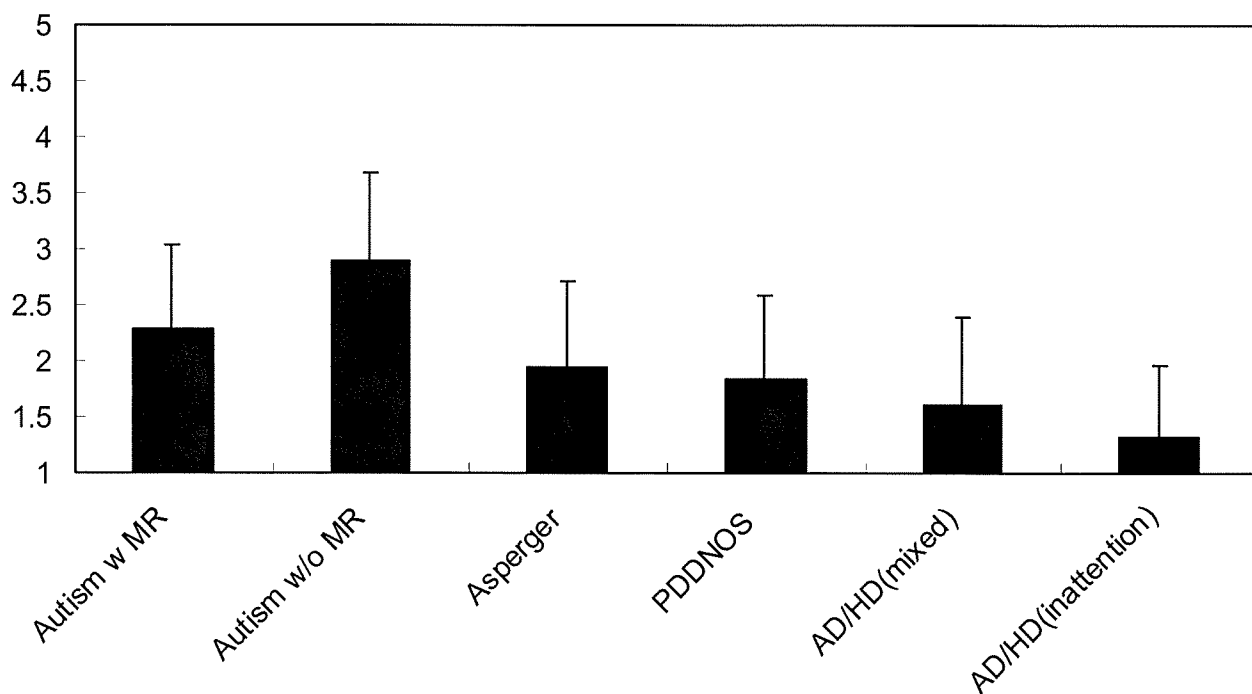
的障害を伴う自閉症群と AD/HD (混合型) 群に対して低い以外は、みられなかった。

睡眠リズム



この項目が最もばらつきも大きく、群間差もみられなかった。

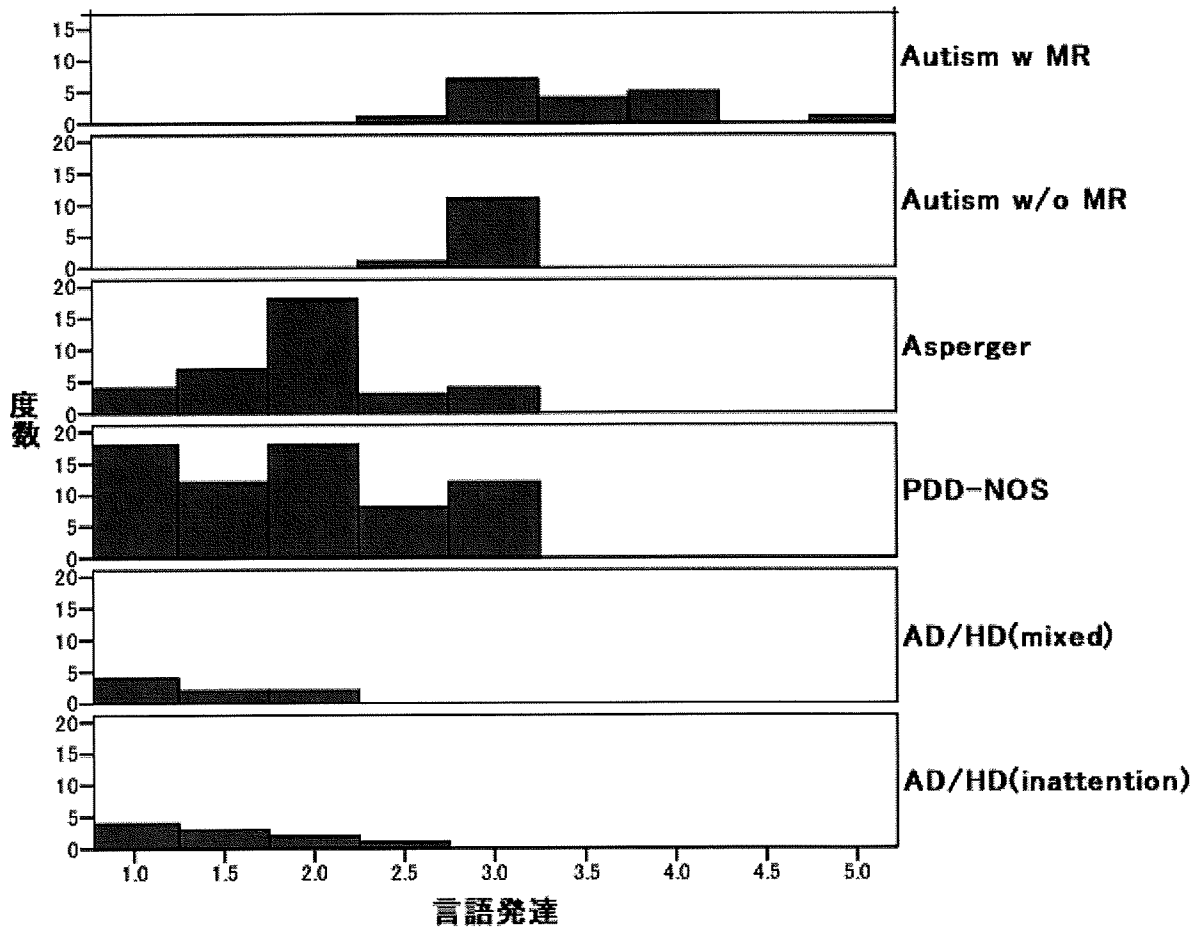
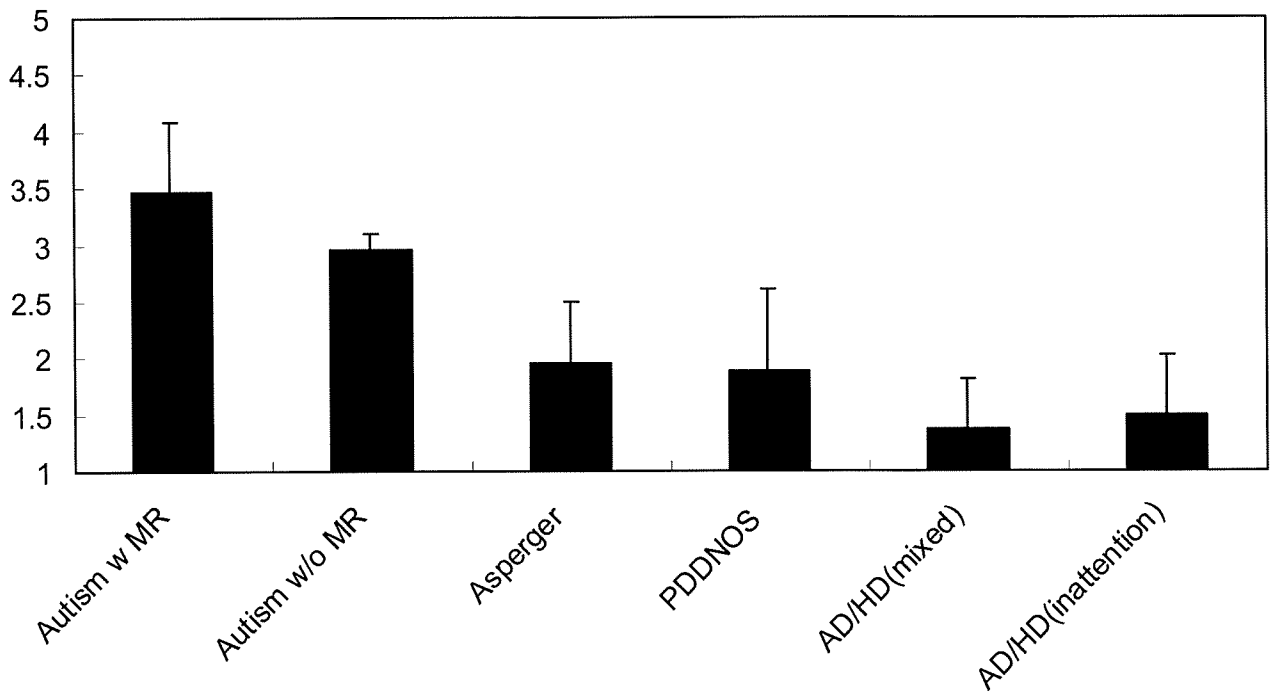
学習障害



高機能自閉症群のみが高く、知的障害を伴う自閉症群以外のいずれの群とも有意であった。しかし、学習障害は幼児では判定していないの

で、特に自閉症群で N が少なくなっており、解釈は要検討である。

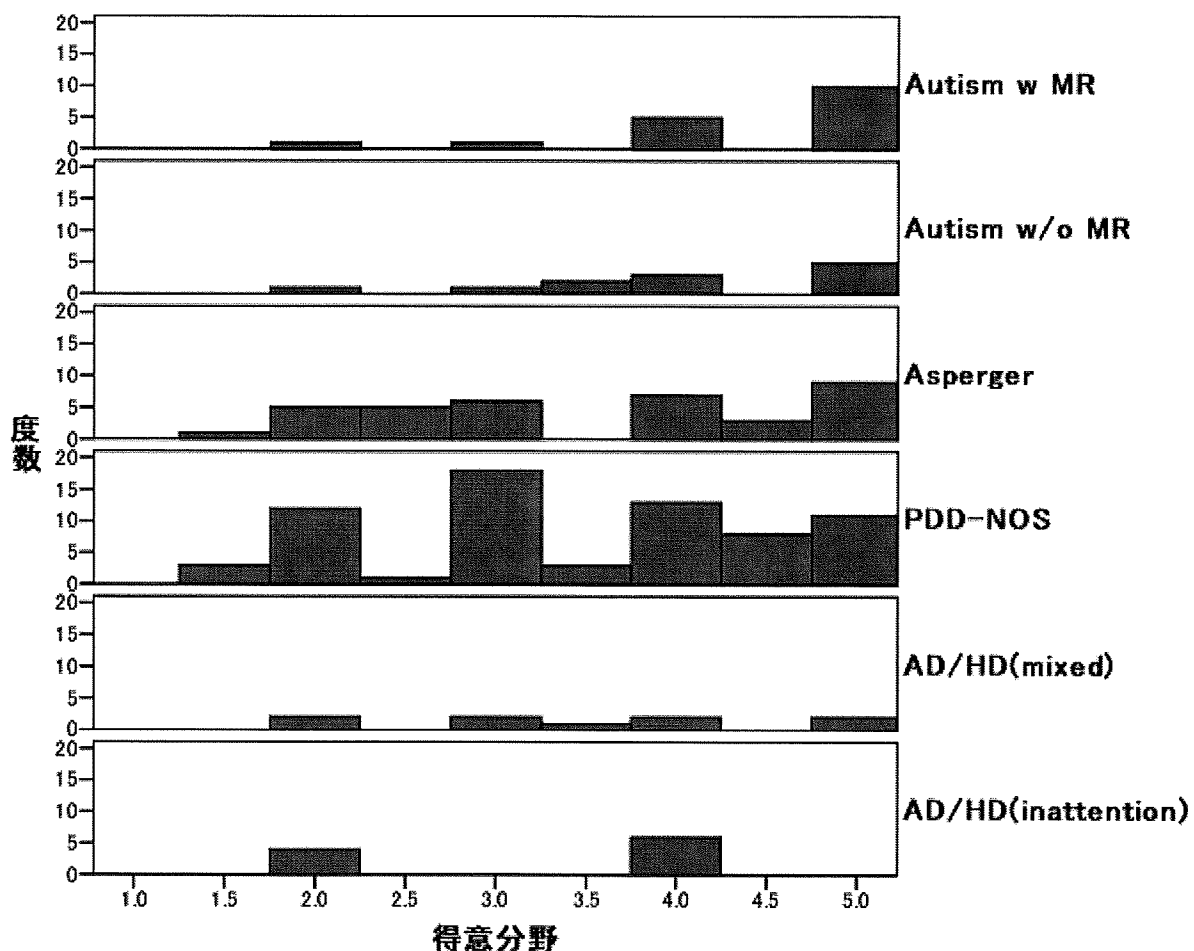
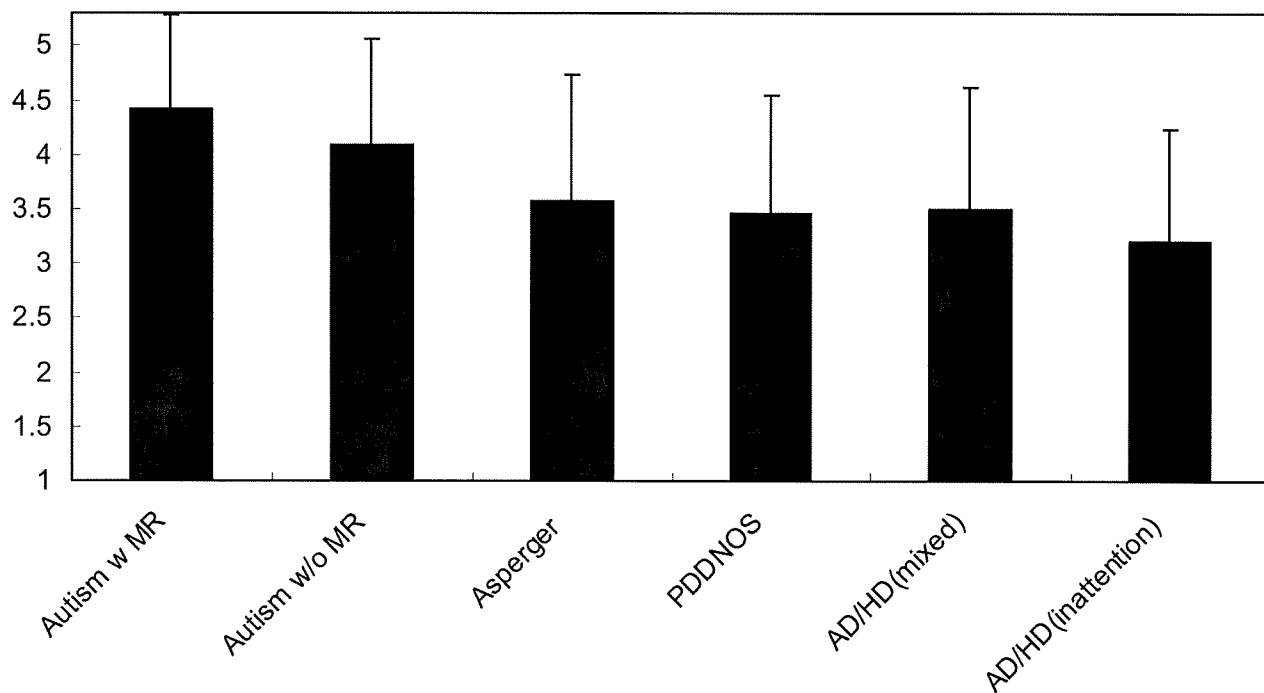
言語発達



自閉症群は定義通り、他のどの群よりも有意に言語発達が遅れていた。自閉症 2 群間では有意差なし。他の 4 群間もみられなかった。アスペルガー障害、PDD-NOS は、言語発達の遅れがないという基準になっているが定型発達の

平均、初語 11 ヶ月、2 語文 21 ヶ月に比べ、初語 15 ヶ月、2 語文 26 ヶ月とやや遅めであった。AD/HD 群は両群とも初語 13 ヶ月、2 語文 22 ヶ月で一般平均と変わらなかった。

得意分野



最も得意な分野において、1;卓越している、5;得意と感じる分野がない、という具合に、どのくらいできるかを評価している。内容、程

度ともかなりばらつきが大きく、内容に関しては、今後、まとめて報告することとする。

D. 考察

本チャートは、発達障害者の支援を目指して作成したものである。第一目的のひとりひとりの特性理解という観点において、本チャートは役立つものであるという印象は受け続け、この目的は達成できそうである。例えば、発達障害という理解しにくい診断名を告げられても、自分のどこがそれに合致するのか、うまく納得できないままであるがために、疾患受容が悪い、と言われてきたが、わかりやすく図示し、得意な分野を積極的に評価していくことで、自分を理解し、自らトラブルを未然に防いだり、ストレスを軽減できたりする方々と出会ってきた。また、診断より先にチャートで特性説明をすることで、診断までの流れがスムーズにもなっている。このように自分自身の理解ばかりか、周囲からの理解も良好となり、共通認識のもとに過ごすことで、無理な負担や叱責が減少したという声もよく聞く。診断名のみが伝わると、「障害」という言葉で自己評価の低下、また、周囲からもとにかく「障害」だから支援をしてあげなければ、という目線になりやすく、支援といってもどう支援したらいいかわからないことも多い。恐らく、「障害」に対する「支援」というより、「特性」を自他共に「理解」といった方が、スムーズではないかと感じている。しかしながら、その目的にどれだけ有用であったかを今年度1年でデータとして示すには至らなかった。なぜなら、本年度は、ひとりひとりに役立つように使用し、試行錯誤しながら、ブラッシュアップを重ねるのに精一杯であったからである。来年度は、使用感のアンケートという形で、種々の立場の方からの感想、意見をまとめていきたい。有効性をしっかり示すには、おそらく、長期フォローアップを行い、2次障害の合併率や就職率などを調べるとよいだろうが、それは今後の課題である。

一方で、議論を重ね一致率を確立したメンバーにより、特性解析を行うことはできた。診断に関しても検討会にて、複数の児童精神科医により確認している。しかし、現時点ではメンバーが限られているため被験者数は上記の通りで、また、外来通院者が主となっているため診断分布にばらつきが見られた。年齢は自閉症で低く、AD/HD（不注意優勢型）で高くなっているが、これはそれぞれの特性の方が、受診される年齢を反映しており、一般外来ではやむをえなかった。というものの、年齢の群間差は小さくなく、自閉症群を除けばみられなかった。また、幼少期まで遡り、その人の生涯特性という観点でスケールリングしているので、年齢の間

題は大きくないと考えているが、今後症例数を増やして年齢別の検討を行いたい。本年度の症例では、17歳以下に絞って検討し直したが、傾向としては変わらなかった、しかし、特にAD/HD（不注意優勢型）群の例数が17歳以下では少なく、解析には至らないばかりか、冊子に掲載する際の差し障りを懸念し、症例集積後とした。

特性別に考察すると、やはり診断基準の主要項目である社会性が群間が分けられやすい。PDD-NOSのうちの多くは（この群の多様性については後述）、一見わかりにくい広汎性発達障害とされるが、社会性の点で理解や配慮が必要なほど困っていることが多い。つまり、広汎性発達障害は全般的に要配慮となるが、やはり、下位診断ごとに程度は異なっている。PDD-NOSは3前後となっており、担任や上司などの責任的立場の人が把握して全体的に配慮をすることで集団に属していくであろう程度、Asperger障害では3.5-4で関わる殆どの人の理解がある集団に属していくであろう程度、自閉症では4-5で集団よりまず快適な個別の社会生活を考えるのがいいのではないかという程度となっていた。

一方、群間に差が見られないのは、睡眠リズムと得意分野であった。これらは、生涯特性としてスケールリングすること自体に無理があったかもしれない。睡眠問題は環境により大きく変化するし、精神科外来では発達障害でなくてもごく一般的である。しかし、睡眠リズムの乱れは無視できない特性であると考えており、今後はできるだけ環境要因を受けにくいスケールリング法を検討したい。得意分野も本来の特性以外の影響を受けやすく、ばらつきの大きさはやむをえないが、発達障害者に見られうる能力を積極的に見いだせるよう、この特性は工夫を重ねながら残していきたい。今回の結果は、どの群も平均3-4.5であり、得意と感じる分野が見つからないか、あっても大したことではないという感じであった。今回、精神科外来を中心としたためかもしれないが、これは、自己評価につながる項目なので、今後検討したい。また、前述したとおり、学習障害の項目は判定が簡単ではなく、慎重な観察や情報収集が必要である。

特性を全体的に見ると、AD/HD（不注意優勢型）は、PDD-NOSに近く、AD/HD（混合型）のみ違う傾向のある特性がいくつか見られた。たとえば、AD/HD（混合型）群のみ、感覚過敏、粗大運動、巧緻性の項目で低く、こだわりもこの群のみやや低めであった。つまり、

不器用さ、発達性協調運動障害の合併が少ないと考えられる。なお、PDD-NOSは、DSM-IVの定義にもあるように非定型自閉症も含むため、幅の広い集団となってしまっている。これが、今回の解析結果にもあらわれ、この群において特にばらつきが大きい。この群の多くが、アスペルガー障害の基準に満たない広汎性発達障害であったが、一部に非定型自閉症を含んでいる。このようなばらつきに対し、PDD-NOS群以外も含め、症例数が十分になった段階で、従来の診断枠を超えたクラスターがないか、クラスター解析を行うことも検討している。

本チャートはこれまで開発段階にあったので、限局したスタッフが使用してきたが、今後の最大の課題は、どれだけの人役に立てるか、ということである。つまり、評価が崩れない形で、どこまで評価者を増やすことができるか、ということであろう。現在は、発達障害を日常的に診療している児童精神科医間での一致率は確立し、ほぼ各評価基準も安定してきた。初版としてはほぼ成立してきたと考えている。今後は、評価者を徐々に増やしていく予定で、一般精神科医の使用を始めている。必要に応じて、注釈を増やししながら、多職種にも広げ、より多くの人の役に立てることを願っている。

E. 結論

発達障害者の理解を自他共に促進し、トラブルを未然に防ぎ、ストレスを軽減して生活できるよう、特性別要配慮度を図示するレーダーチャートを開発した。現在、児童精神科医間で一致率を確立し、チャートの原案自体もほぼ安定している。また、得られたデータで、各特性における診断名別の解析を行い、各群の特徴を示した。

F. 健康危険情報 なし。

G. 研究発表

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H. 知的財産権の出願・登録状況
なし。

研究成果の刊行に関する一覧表

雑誌

発表者氏名	論文タイトル名	発表誌名	巻号	ページ	出版年
Funabiki Y & Funabiki K	Factors limiting song acquisition in adult zebra finches	Dev Neurobiol (previously J Neurobiol)	69(11)	752-9	2009

Factors Limiting Song Acquisition in Adult Zebra Finches

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ABSTRACT: Song learning takes place in two separate or partially overlapping periods, a sensory phase in which a tutor song is memorized and a sensorimotor phase in which a copy of the model is produced. The stage of song development where song becomes stable and stereotyped is called crystallization. Adult birds usually do not learn new song in many species including the zebra finch. However, it is not known whether song crystallization as such or aging impedes adult learning. Exposure to loud noises prevents birds from developing and

crystallizing their song, because they cannot control their voice by auditory feedback. Zebra finches even without previous experience of hearing or singing a song failed to learn a song model provided in adulthood. Thus, neither the absence of a tutor song nor the lack of song crystallization enables new song learning in adulthood, but age *per se* limits the ability or motivation to learn song.

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Keywords: songbird; adult learning; sensitive period; zebra finch; crystallization

INTRODUCTION

The development of birdsong and human speech share some features; young birds copy song from adult tutors; song is a complex sound used for communication between individuals, and its learning is restricted to youth in species which have been studied in laboratories. In zebra finches, one of the species commonly used in songbird research, young birds begin to memorize a tutor song as early as 25 days of age (Immelmann, 1969). Young zebra finches usually

memorize a tutor song before 65 days of age, although those birds that are either untutored or given a hetero-specific tutor song may still learn a conspecific song at ages of 65–80 days (Immelmann, 1969; Eales, 1985; Aamodt et al., 1995; Livingston et al., 2000). Zebra finches usually start to sing after 35 days of age and crystallize their song by 90 days of age, beyond which even birds reared by parents of other species do not learn the conspecific song (Immelmann, 1969). Once zebra finches developed their own song, they do not learn new songs even when the song is “decrystallized” by exposure to loud noises (Zevin et al., 2004). Untutored birds also crystallize their songs by 90 days of age, although they tend to sing abnormal and simple songs. Such birds may incorporate a part of a new tutor song heard after 120 days of age into their crystallized song (Eales, 1985; Morrison and Nottebohm, 1993; Jones et al., 1996).

Thus, learning tends to decline after song crystallization, irrespective of the experience of tutoring.

Additional Supporting Information may be found in the online version of this article.

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However, because song crystallizes with age, it is not known whether song crystallization *per se* or aging affects the ability or motivation to learn or modify song. If we can control the age of song crystallization, we should be able to discriminate between the effects of aging and those of song crystallization on vocal learning. Exposure to continuous noise during the normal sensorimotor period delays song development. Zebra finches whose song development is artificially delayed by as much as 3 months can reproduce the tutor song that they memorized before 35 days of age (Funabiki and Konishi, 2003). This work shows not only how long zebra finches can remember tutor song but also how birds of this age can use auditory feedback to control vocal-motor output according to the acquired song template. A corollary question is whether we can teach a song to finches older than 100 days of age without previous experience of hearing or crystallizing song. The present report addresses this issue.

METHODS

Animals

All procedures were approved by the Animal Care and Use Committee of the California Institute of Technology. We set up three breeding pairs of zebra finches in individual sound attenuated chambers to obtain 17 nestlings. Figure 1 shows the design of experiments. After their fathers had been removed at 2–5 days of age, their mothers alone reared the young birds until 35 days of age. We used four of these birds as controls to confirm that our tutoring apparatus works successfully, although previous reports show that not only seasonal singers but also zebra finches can

learn from playback (Marler and Peters, 1988; Houx and Ten Cate, 1999; White, 2001; Phan et al., 2006). The remaining 13 birds were experimental birds. The mothers of both groups were removed at 35 days of age and then young birds were kept in individual sound-attenuated chambers throughout the experiment.

After isolation, we immediately began to expose the 13 experimental birds to a continuous loud noise of 110 dB (SPL) to prevent them from hearing their own voice. This noise exposure impedes song development and results in deaf-like vocalizations without elaborate sound pattern immediately after noise cessation (Funabiki and Konishi, 2003). The auditory sensitivity of the noise-exposed birds recovers within a week after the cessation of noise exposure.

Tutoring with Playback of Recorded Songs

The control birds heard the tutor song from 10 to 135 ± 6 (mean \pm standard deviation) (127–141) days of age. The experimental birds heard it immediately after noise cessation at 137 ± 34 (101–200) until 264 ± 76 (192–433) days of age. Three of the four control birds and seven of the thirteen experimental birds heard the same zebra finch song, which differed from the songs of their fathers. The remaining birds heard the same Bengalese finch song. We used a Bengalese finch tutor to distinguish the learned parts from the species-specific components of song clearly (tutors in Fig. 2).

The tutor songs were played in individual sound-attenuated chambers with a computer system in the same way as the previous report (Funabiki and Funabiki, 2008). We conducted two daily tutoring sessions, one in the morning (starting at 8 AM 30 min after light-on) and the other in the afternoon (at 5 PM). In each session, each song file of 2.8 s was played seven times with 1-min interval. The song file of the zebra finch tutor song had three motifs and the Bengalese song did not consist of motif structure (see Fig. 2).

Song Recording and Analysis

The songs of pupils were recorded on the day of starting and ending of tutoring. The same set of instruments, methods, and parameters of song analysis was used for comparison of results between the present and previous studies (Funabiki and Konishi, 2003; Funabiki and Funabiki, 2008). Shortly, we analyzed similarity of phonology (acoustic features) between a tutor and a pupil song using the software Sound Analysis 2.08 by Tchernichovski et al. (2000). The song files used for similarity analyses were 1 s in duration for the tutor and 3 s for the pupils. The longer sample from the pupils reduced variability in similarity scores. We obtained mean similarity scores for ten randomly selected song files per bird per sampling day. We also analyzed similarity of syllable sequences in controls. We randomly selected 50 songs including 1500–2000 syllables from each bird. We defined the similarity of sequences as the probability that syllable transition coincidences between tutor and pupil syllable sequences. That is, we

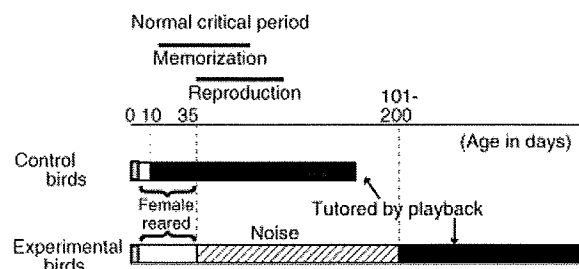


Figure 1 Schema of the experimental procedures. Fathers were removed when their nestlings were 2–5 days of age in both groups and then all birds were reared by mothers only until 35 days of age. Control birds heard a tutor song from playback since 10 days of age. Experimental birds were exposed to loud noise from 35 days of age. After the release from noise, birds started to hear a tutor song for the first time, and gradually developed songs afterwards.

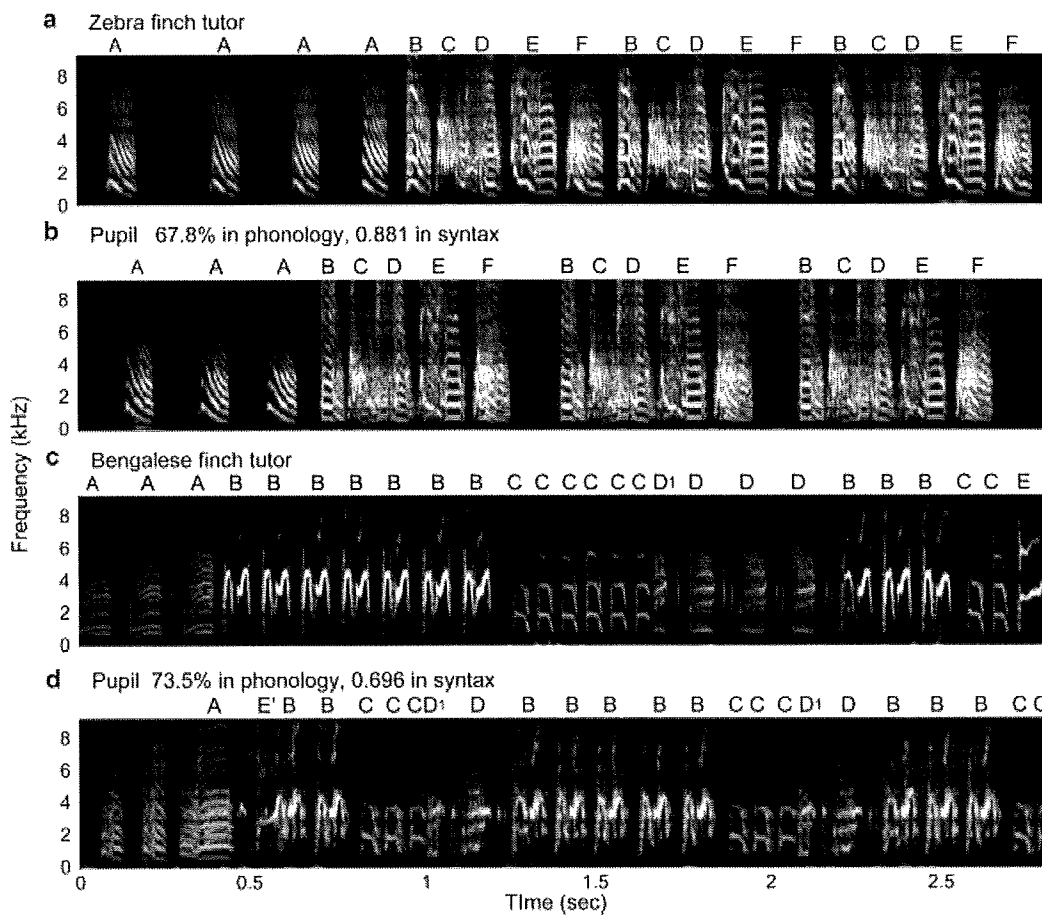


Figure 2 Songs of control birds tutored with a playback song from 10 days of age. Control bird (b) was tutored with a zebra finch song (a) and another control bird (d) was tutored with a Bengalese finch song (c). All birds learned well both syllables and their sequences in playback songs. Each syllable in the tutor song was labeled with a letter and the syllables copied into the pupil song were also labeled with the corresponding letters. When only a part of a syllable was copied, a dash was inserted after the letter. Similarity scores of phonology and syntax are shown in the figure.

overlapped the tutor and pupil distributions of transition probabilities of every syllable pair. The score of 1 means that the tutor and pupil sequences are identical. We did not calculate the similarity of syllable sequences in experimental birds, because good copying of each syllable is a prerequisite for that analysis.

We used Sound Analysis also for quantifying the acoustic features of songs, including pitch, entropy, frequency modulation, continuity, syllable duration, motif duration, syllable number in song, and syllable number in a motif. Since we did not see significant differences between the control birds tutored by a live-tutor (from the control group in the previous article: Funabiki and Konishi, 2003) and those tutored with a playback song (control birds in this paper) in the series of analyses, we combined them to use as the control group for the analyses in syllable features (White, 2001; Phan et al., 2006). Also, because several acoustic features are apparently different between the zebra finch and the Bengalese finch song (e.g. pitch, entropy), we analyzed

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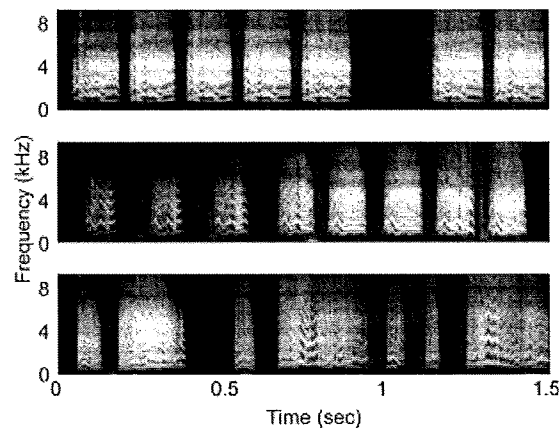


Figure 3 Vocalizations just after noise in experimental birds. When experimental birds were released from noise, they vocalized like deafened birds. Their songs had neither rhythmic patterns like motifs nor fine structures in syllables.

songs of birds that heard the zebra finch model separately from those that heard the Bengalese finch model.

We needed to adjust the parameters of Sound Analysis to our colony. The parameters are as follows: FFT option is as default [Window size 409 samples of sound (9.3 ms), overlap 0.85, Bandwidth 1.5, FFT size 1024, Tapers 2, Frequency range 11025 Hz], pitch calculation in Feature Calculation is 3445 Hz by Median contours interval, Feature weight is as default (1:1:1:1), time warping tolerance is also as default (0.35), Contour contrast is 1, Contour power is 0, and similarity score options are as default (threshold 92%, interval 70 ms, section 20 ms). Because the songs of zebra

and Bengalese finches are quite different, they needed two different sets of score options for our colony. Score options for zebra finches are as follows (mean, absolute median deviation): pitch 1555 Hz, 655 Hz; FM 38.8 degrees, 20.5 degrees; entropy -4.16, 0.67; continuity 0.827, 0.119. Score options for Bengalese finches are as follows: pitch 2100 Hz, 1189 Hz; FM 36.1 degrees, 22.9 degrees; entropy -4.48, 1.11; continuity 0.823, 0.151.

Since the range of similarity scores differed between the two species used, we scaled the scores from the Bengalese finch setting to those of the zebra finch setting. We used similarity scores of crystallized songs in 10 zebra and 12

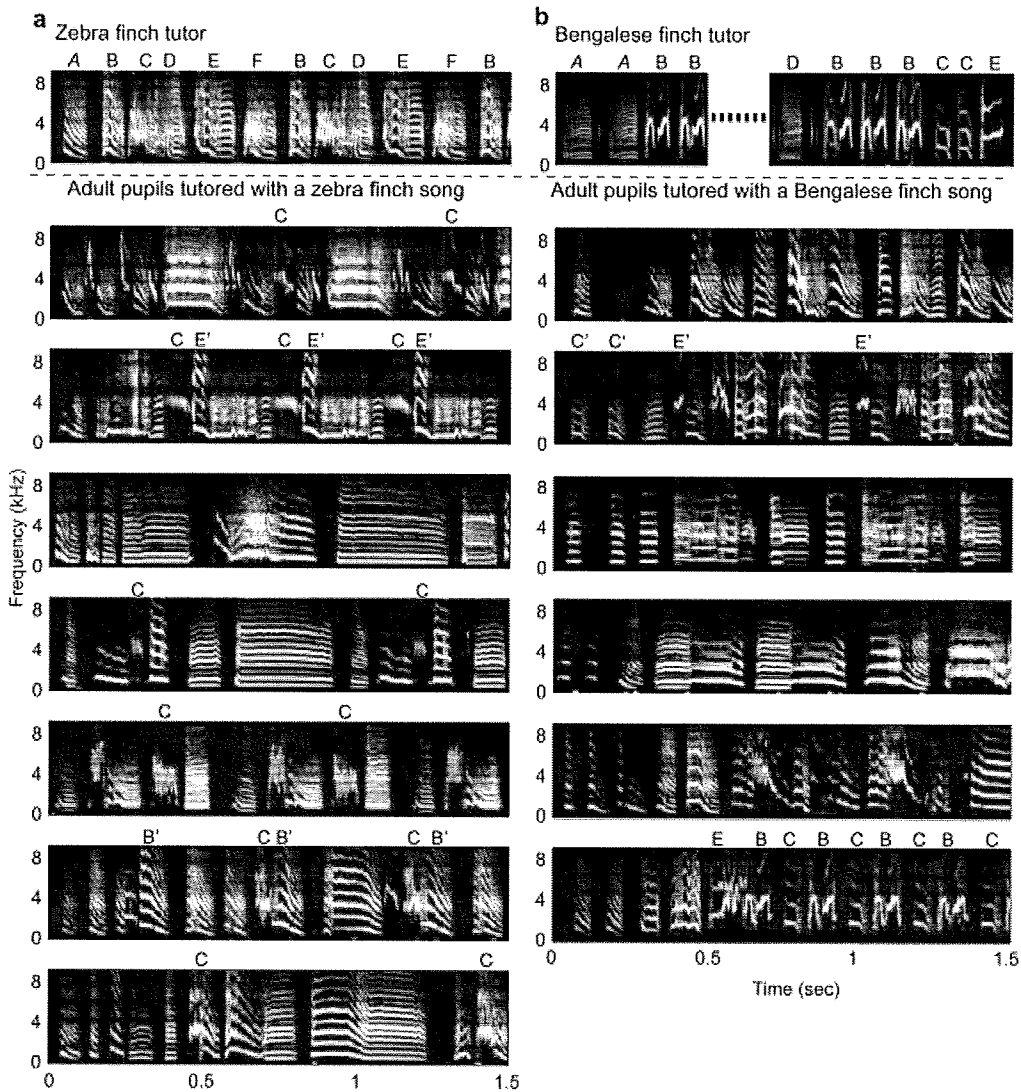


Figure 4 Songs after tutoring in adulthood. Each sonogram is from a different bird. The top sonograms are tutor songs. The left column shows the songs of birds tutored with the zebra finch song, and the right column shows those tutored with the Bengalese finch song. Syllables were labeled as in Figure 2. Pupil syllables corresponding to introductory notes (A) in the tutor songs were not labeled, because birds produce such syllables without learning. One experimental bird at the right bottom in the figure copied the tutor syllables well, but the syntax was different. Songs of the other experimental birds were dissimilar to the tutor song.

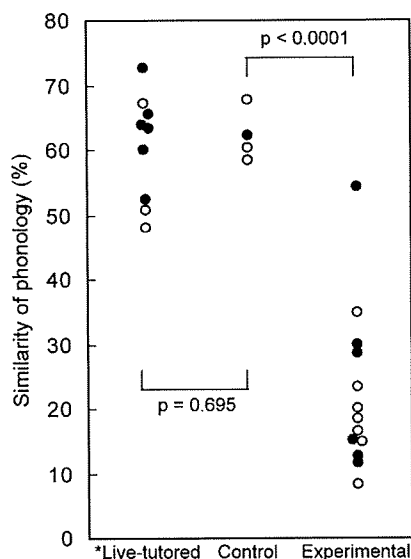


Figure 5 Similarity of syllable phonology to the tutor. One group of birds was tutored with a zebra finch song as indicated by open circles and another group with a Bengalese finch song as indicated by closed circles. Control birds, which were reared only by their mothers and tutored with a recorded song from youth, learned the song as well as live-tutored birds in the previous study, which were reared by both parents and not exposed to noise. Songs of experimental birds showed much lower similarity scores. Live-tutored birds were from the control group ($n = 9$) in the previous experiment (Funabiki and Konishi, 2003; see Methods).

Bengalese finch-reared birds for the scaling. They were from experimental and control groups from the study by Funabiki and Konishi (2003). We measured the floor noise and the mean of the similarity scores for each of zebra and Bengalese finch settings. The mean scores for zebra and Bengalese finch settings were 57.04 and 70.26, respectively. The floor noise, that is, the expected similarity scores of two totally uncorrelated songs, was cross-calculated using these songs. The floor noise of zebra finch setting was 18.11, the mean similarity score of songs of 12 Bengalese finch-reared birds to the zebra finch model. The floor noise of Bengalese finch setting was similarly calculated as 45.07. We set the floor noise and the mean score of Bengalese finch setting to those of zebra finch setting and scaled linearly all the similarity scores from Bengalese finch setting. The scores of 13 experimental birds in the present study did not differ between the zebra finch- and the Bengalese finch-tutored groups ($p = 0.281$; unpaired t -test).

RESULTS

Learning Song from Playback in Our Apparatus

The songs of the controls that learned from playback were similar to the tutor song (Fig. 2, Supporting Information Sounds 2a–2d). The mean of similarity

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scores of phonology in these birds was 62.1 ± 4.1 . These similarity scores were not significantly different from those of live-tutored birds studied by Funabiki and Konishi (2003) ($p = 0.695$; unpaired t -test: in four control and nine live-tutored birds; cf. Fig. 5). These nine birds were the controls in the above-cited study. These birds were reared by live tutors until 35 days of age and isolated individually without exposure to noise. The mean similarity score of syllable sequences in the four birds was 0.623 ± 0.209 (1 = perfect), which was also as high as 0.655 ± 0.128 in the nine live-tutored birds ($p = 0.733$; unpaired t -test). Thus, birds can learn songs in our tutoring apparatus as in other studies (Houx and Ten Cate, 1999; Phan et al., 2006).

Adult Birds Without Previous Song Experience Copied Syllables Only Sporadically

The vocalizations by these birds just after noise cessation resemble those of the birds exposed to loud

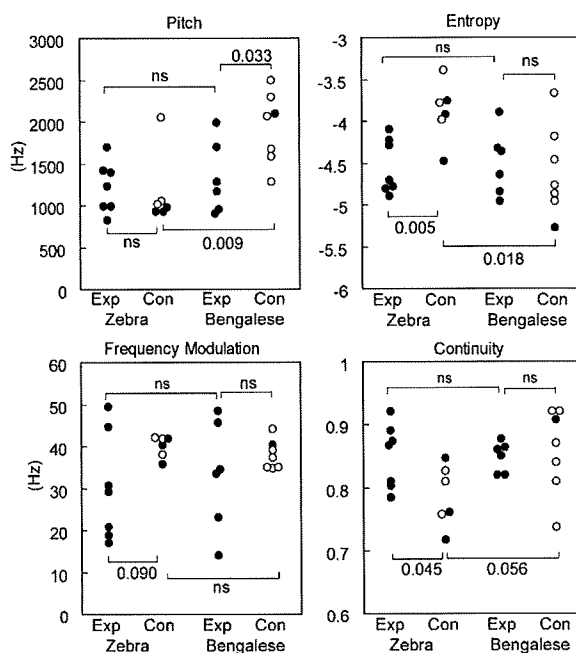


Figure 6 Comparison of song acoustic features between experimental and control birds. We analyzed pitch, entropy, frequency modulation, and continuity of songs. Exp means experimental birds ($n = 7$, zebra-tutored; $n = 6$, Bengalese-tutored) and Con means control birds ($n = 6$, zebra-tutored; $n = 7$, Bengalese-tutored). Numbers indicate p -values of unpaired Student t -test and ns means “not significant.” Open circles in control groups indicate data in birds reared by live tutors, and closed circles are those tutored with a playback. Note that none of the features analyzed showed significant difference between the experimental birds tutored with the zebra finch model and those tutored with the Bengalese finch model.

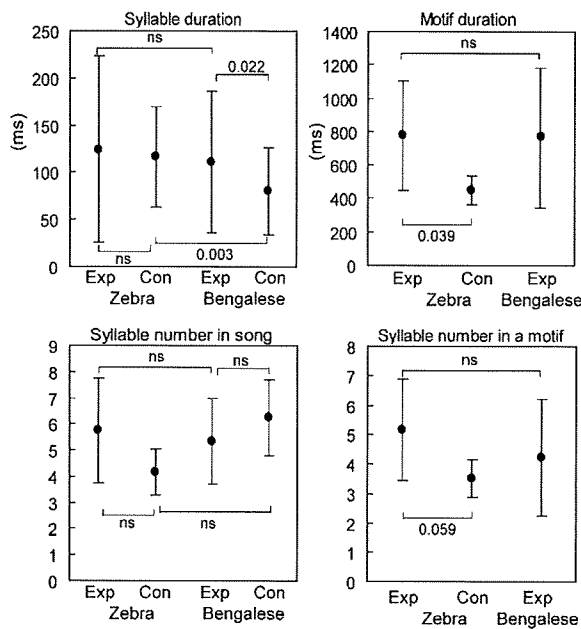


Figure 7 Comparison of the number and length of syllables. Black points indicate the mean and bar indicates the standard deviation. Abbreviations and the number of birds are the same as in Figure 6. We did not measure motif duration and the syllable number in a motif in songs of control birds tutored with a Bengalese finch song, because Bengalese finch song usually does not show a motif structure. Note that experimental birds showed large variance in all the features presented in this figure.

noise from 35 days of age as reported by Funabiki and Konishi (2003), which were like those of deafened birds consisting of noisy syllables without a motif structure (Price, 1979) (Fig. 3, Supporting Information Sounds 3a–3c). Since adult birds with such vocalizations in our previous article developed songs in a similar time course to normal birds, the result that the birds in the present study vocalized like deafened birds not only indicates that the continuous noise exposure successfully impedes song practice, but also indicates that these birds will develop songs afterwards.

After the masking noise was turned off, the birds were tutored. The songs after 127 ± 61 days of tutor-

ing are shown in Figure 4 (Supporting Information Sounds 4a pupil 1–4a pupil 7 and 4b pupil 1–4b pupil 6). These songs contained few characteristics of the tutor song except for one bird that copied syllables from the Bengalese tutor song well, although it did not imitate the syllable sequence How about (Fig. 4b, bottom). Their songs also did not contain any components of the song of their fathers, who were removed when the chicks were 2–5 days of age. The mean similarity scores of phonology were 22.1 ± 12.4 in the 13 birds. These scores are lower than those of the control birds tutored by playback song from youth ($p < 0.0001$; unpaired *t*-test: Fig. 5). If we exclude the score of 54.3 for the bird that learned well, the mean score becomes 19.4 ± 8.1 . Thus, the incorporation of song material is impaired in adult zebra finches without any previous song experience of hearing or singing.

We further analyzed several features of songs in experimental birds and compared them with those of control birds (see Methods, Figs. 6 and 7, Tables 1 and 2). In all the features examined, we did not see any statistically significant difference between the songs of the experimental birds tutored with the zebra finch model and those tutored with the Bengalese finch model. In contrast, we found significant differences in pitch, entropy, and syllable duration between the songs of the control birds tutored with the zebra finch model and those tutored with the Bengalese finch model. Also, the songs of experimental birds showed large variances in many features, including frequency modulation, syllable duration, and the number of syllables (see Fig. 7). Furthermore, these birds sang songs with low entropy, high continuity, low frequency modulation, and the large number of syllables, as compared with the control birds that heard the zebra finch model. The mean of syllable lengths did not differ between the songs of the experimental and those of the control birds that were tutored with the same zebra finch song. However, the experimental birds frequently produced long call-like notes. The songs of six out of the 13 birds had such notes longer than 200 ms in duration (see Fig. 4) as in the songs of isolated birds reported by Price (1979),

Table 1 Feature Analysis of Songs

	Pitch (Hz)	Entropy	FM (Hz)	Continuity
Zebra-tutored				
Experimental	1216 ± 306	-4.54 ± 0.33	30.0 ± 12.7	0.85 ± 0.05
Control	1157 ± 440	-3.88 ± 0.36	39.9 ± 2.5	0.79 ± 0.05
Bengalese-tutored				
Experimental	1332 ± 433	-4.51 ± 0.39	33.1 ± 13.1	0.85 ± 0.02
Control	1917 ± 427	-4.60 ± 0.54	37.9 ± 3.5	0.86 ± 0.07

Numerical values of mean \pm standard variation for each acoustic feature of songs shown in Figure 6 are listed.

Table 2 Syllable Number and Duration

	Syllable Duration (ms)	Motif Duration (ms)	Syllable Number in Song	Syllable Number in a Motif
Zebra-tutored				
Experimental	124 ± 99	776 ± 329	5.8 ± 2.0	5.2 ± 1.7
Control	117 ± 53	450 ± 87	4.2 ± 0.9	3.5 ± 0.6
Bengalese-tutored				
Experimental	111 ± 74	764 ± 420	5.3 ± 1.6	4.2 ± 2.0
Control	80 ± 46	–	6.3 ± 1.5	–

Numerical values of mean ± standard variation of parameters shown in Figure 7 are listed.

although those long notes are rarely seen in normal song (Morrison and Nottebohm, 1993).

DISCUSSION

Studies that address the separation of song crystallization and age already exist in seasonal singers. Nottebohm (1969) reported that a castrated chaffinch, which failed to sing in their first year, could learn song in the second year as revealed by treatment with androgen. Whaling et al. (1995) showed that injections of testosterone to young white-crowned sparrows induced premature song crystallization, which resulted in songs that did not resemble the song of their tutor. Also, these birds produced the same abnormal song when they sang naturally in the following spring. These studies lend support for the idea that song crystallization not only marks the end of vocal development but also is the cause for the inability to learn new song afterwards. However, the present work shows that the learning of a new song is limited even in adult zebra finches without crystallized song.

All but one experimental bird failed to copy the tutor song despite many days of tutoring. After noise cessation, they began their song development and crystallized their songs over 1 month. That is, song crystallization had been postponed well into adulthood. Their crystallized songs were not like those produced during the noise exposure, but showed some of the features (existence of very long notes, abundance of call-like notes, slightly high pitch) reported in birds raised in isolation (see Figs. 4, 6, and 7; Price, 1979; Morrison and Nottebohm, 1993; Aamodt et al., 1995; Livingston et al., 2000; Kojima and Doupe, 2007). Also, we did not see any statistically significant differences in the features analyzed between birds tutored with the zebra finch model and the Bengalese finch model. These results might indicate that adult zebra finches without any previous song experience retain and use the innate song template, which is usually modified or replaced by a tutor model in youth (Konishi, 1985), even if a normally

highly acceptable tutor model is provided during song development.

The differences between the control and the experimental birds are the age of hearing a tutor song and the experience of noise exposure. A long period of exposure to loud noises does not leave irreversible effects on hearing or erase the memory of a tutor song in zebra finches (Funabiki and Konishi, 2003). Also, adult zebra finches, irrespective of the previous exposure to loud noise, correct their syllables upon hearing the original tutor song in adulthood (Funabiki and Funabiki, 2008). Thus, exposure to loud noises does not seem to have irreversible effects on brain circuits involved in song development and maintenance. Therefore, we assume that the declined song learning observed in the experimental group is due to age or age-related changes in brain circuits.

In conclusion, although zebra finches can retain the memory of tutor song far beyond the normal onset of song development, their ability or motivation to incorporate a new song declines with age irrespective of previous auditory or vocal experience.

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